Do Arthropod Prey Alter Behavior When Exposed to Different Combinations of Sensory Cues from Predators?

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Do Arthropod Prey Alter Behavior When Exposed to Different Combinations of Sensory Cues from Predators?

by

Kelly I. Pniewski

A Master's Thesis Submitted to the Faculty of

Montclair State University

In Partial Fulfillment of the Requirements

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DO ARTHROPOD PREY ALTER BEHAVIOR WHEN EXPOSED TO DIFFERENT
COMBINATIONS OF SENSORY CUES FROM PREDATORS?

A THESIS

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Montclair, NJ

2014
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Abstract

How animals respond to predatory threats is influenced by the kinds of sensory cues from predators they are able to detect. Because sensory information is transduced through the environment, both that and the animal’s physiology may determine how animals are capable of reacting and are important variables when considering their behavioral responses. In this study I tested the effects of visual, chemical and seismic predator cues on how prey react to predatory threat. Four species of arthropod prey animals were tested; German cockroaches, *Blatella germanica* (Blattodea: Blattellidae), House crickets, *Acheta domesticus* (Orthoptera: Gryllinae), Pill bugs, *Armadillidium vulgare* (Oniscidea: Armadillidiidae), and Sow bugs, *Porcellio laevis* (Oniscidea: Porcellionidae) in the presence of predatory spiders. Seismic cues were more significant than visual, chemical cues or a combination of the two in driving prey behavior when prey were exposed to predators. There is also a significant behavior difference when prey were exposed to predatory threat without barriers as providing barriers induces an unnatural or muted response. These results indicate that the physiologies of the arthropod prey used in this study are more effective at mechanoreception than visual reception or chemoreception.
Introduction

Predator detection can be costly for animals because if ignored they can increase mortality risk, but if not they can diminish opportunities for foraging and reproduction (Lima & Dill 1990). For example juvenile *Notonecta hoffmanni* (Hemiptera: Notonectidae) spent significantly less time in a given foraging area when predatory adults were present (Sih 1982). Regarding reproduction, higher risk taken by adult individuals is found in the marine fish *Gobius niger*, where young males refrained from courting females when exposed to a predator, while older males reproduced under the same conditions (Magnhagen 1990). How quickly an animal can recognize a potential threat and act upon it may minimize these costs. Recognizing appropriate sensory modalities from predators therefore is essential for the initiation and proportionality of anti-predator response (Cooper 2006).

Sensory ecology of predator avoidance in arthropods

The phylum Arthropoda comprises the largest animal taxon in numbers and species diversity (Ødegaard 2000). Though there is much literature describing their reproduction, life histories, diets and feeding habits, ecological importance and many other aspects of their physiology and behavior there are fewer studies describing predator-prey interaction and its importance (Lardies et al. 2004, Philpott & Armbrecht 2006).

Arthropods, like all other animals, receive cues through tactile, chemical, visual and auditory means. They have specific sensory processes for detecting these cues. For example, arthropod antennae can function as mechanoreceptors that are used to detect tactile cues as well as chemoreceptors that receive chemical cues. American
cockroaches, *Periplaneta Americana*, (Blattodea: Blattidae) use their antennae, specifically the distal flagellum, to detect and to maintain a constant distance from a wall as they walk or run along it. Cockroaches have also been observed increasing speed the closer they were to the walls and using their antennae to avoid protrusions (Camhi & Johnson 1999).

Animals react differently to specific cues and then act in accordance with the nature of the threat. Tactile and chemical cues may be direct or indirect, whereas visual and auditory cues come directly from the predator. For example, in a study conducted using *Tetranychus urticae*, Two-spotted spider mite, (Trombidiformes:Tetranychidae) as prey and *Phytoseiulus persimilis* (Mesostigmata:Phytoseiidae) as predatory mites indirect chemical cues were provided to female *T. urticae* as discs that predatory female *P. persimilis* had previously spent 24 hours on as well as discs not exposed to the predatory mites. When offered a choice to deposit their eggs on either substrate *T. urticae* chose less often discs that previously held the predatory mites when exposed less than 24 hours. The chemical cues dispersed after 24 hours and no longer dissuaded *T. urticae* (Dicke & Grostal 1999). This experiment tested the importance of chemical cues as well as the durations indirect cues may last in the environment. Though some chemicals may persist for hours others may disperse quickly depending on wind, humidity and other environmental factors. It is important for animals to be able to assess the potential danger of these cues while they are still present.
Vision

There are two structurally different kinds of arthropod eyes; compound eyes with multiple lenses (e.g. insects and crustaceans) and simple eyes with a single lens (e.g. spiders and scorpions). Within these two categories the possible variations in the structural features are enormous. Such variable parameters include eye size, shape, retinal sampling density and construction, visual field size, aperture size, spectral and polarization sensitivity (Warrant & McIntyre 1993). Compound eyes suffer from diffraction limit, or having a maximum limit of angular resolution, but can bypass this limitation with three acute zones of higher resolution dependent upon regions of the environment that may be of particular importance to that species or sex. The distribution of acuity has been affected by several variables such as the capture of prey, the capture of females for mating, as well as the way the image flows across the eye of the during flight (Goldsmith 1989).

Preying mantids have large binocularly overlapping acute frontal-dorsal zones that are used to center potential prey before they strike. Mantids provide the only known example in insects where prey distance is determined by binocular triangulation (Rossel 1983). There are also examples of male Dipteran flies of forward-pointing acute zones that are used for chasing and catching females. Male house flies, *Fannia eanieularis*, (Diptera: Fannidae) keep the females in the dorso-frontal region while chasing them and continuously adjust their path so as to keep the female ahead (Land and Collett 1974; Wehrhahn 1979; Wagner 1986).
Dorsal acute zones are used in small signal detections, such as a dark spot on a white background. Males of swarming insects tend to have the more extensive dorsal acute zones along with more noticeable sexual dimorphism. There are few examples of acute dorsal zones in crustaceans, but there has been documentation of the carnivorous cladoceran *Polyphemus*, that hunt in swarms, using its single (fused) compound eye to locate and track swimming prey (Young & Taylor 1988). Among insects, there is a large variety in the distribution of resolution across the eyes of different dragonflies that have to do with their lifestyles. In slower flying zygopterans there is only a weakly developed frontal acute zone, whereas in the faster-flying group of corduliids this is more pronounced (Sherk 1978).

Arthropods with simple eyes, such as arachnids, differ from those with compound eyes in that simple or lens eyes have greater angular resolution that is thought to be more useful for pattern recognition, whereas compound eyes have poorer resolution and are thought to be more specialized for movement perception (Kirschfeld 1976). Wolf spiders for example have eight simple eyes; two primary eyes with moveable retina at the front that form images and six smaller secondary eyes that detect peripheral movement and have a reflective *tapetum lucidum* that enhances night vision. The *tapetum lucidum* is a layer of tissue in the eye located immediately behind the retina that reflects visible light back through the retina and increases light availability to the photoreceptors (Ollivier et al. 2004).
Many insect orders, such as Hymenoptera and Diptera, have simple dorsal ocelli. Dorsal ocelli are light sensitive organs that are used in cooperation with compound eyes and consist of a cornea and photoreceptors. Dorsal ocelli are often larger and round in flying insects and found in triplet that they use to detect the horizon, and smaller and flat in terrestrial insects and found in a pair (Bitsch & Bitsch 2005).

Stemmata, or lateral ocelli, are found in the larval forms and certain adult orders of insects, such as Siphonaptera (fleas), Thysanura (silverfish and firebrats) and class Collembola (springtails). Within the stemmata retinula, there are clusters of photoreceptor cells that lie behind each biconvex lens. Stemmata can also be found in Myriopods (Bitsch & Bitsch 2005).

Arthropods have varying degrees of visual perception depending on species or family as well as environmental factors (Mallock 1894, Nordström 2012). For example, mantids use a series of 10 visual characteristics when evaluating potential prey including; overall size, length of leading edge, contrast with background, location within visual field, and apparent speed (Kral & Prete 2004). Mantids have a visual range of 20 meters and generally hunt during the day out in the open, along the substrate or among plants where keen eyesight is a necessity. They also can have up to 10,000 ommatidia that contain clusters of photoreceptor cells surrounded by pigment and support cells (Prete 1999). In comparison, arthropods that inhabit darker environments underneath rocks, brush or leaf litter would not rely so heavily upon eyesight for either hunting or predator avoidance strategies. Terrestrial isopods (Oniscidea) are found in these environments and have
simple compound eyes. It is likely they do not rely on sight or at least sight alone to
determine predatory threat.

Though visual signals can be highly valuable they do have their limitations. Direct line of
sight and a certain amount of light is necessary to detect the signal. Visual signals also
suffer from poor persistence that only last as long as the sender is signaling. Depending
on the environmental circumstances other cues may be imperative when responding to a
potential threat.

**Chemoreception**

Animals receive chemical information through olfaction, gustation or a combination of
both. Olfaction, an indirect cue, is the detection of chemical cues that are dissolved in
media as in air or water found away from their original source, whereas taste, a direct
cue, is the attainment of cues by direct contact with the source of the cues (Mustaparta
1984, Städler 1984). Direct chemical cues are associated with exuvia, secretions,
excrement or any part of the predator encountered by the prey animal (Kortet & Hedrick
2004). Indirect cues may come from the scent of dead or injured conspecifics (Kats &
Dill 1998).

Olfaction sensory information is obtained through an arthropod’s chemoreceptors that
can be found on the cuticle as well as antennae. Chemoreception is used not only for
predator detection, but also locating food or potential mates, heat, vibration or air
movement. Antennae are located on the first segment in arthropods and are biramous in
crustaceans and uniramous in all other groups. Crustaceans also have a second smaller
pair called antennules. Antennae are adapted with sensilla that detect chemical and mechanical stimuli, though to what degree may depend on the organism. Insect antennae have three segments: scape (base), pedicel (stem), and the flagella (Keil 1999). In all arthropods olfactory receptors on the antennae bind to molecules in the air or water such as pheromones or odors that allow the organism to respond effectively if prey is nearby, a predator, or potential mate.

Chemical signals are generally highly efficient as they tend to have a long range and high persistence. Chemical signals can suffer a slow travel speed however and locating who or what left the signal can be impossible for the receiver. The range of the signal can also vary with environment. For example in marine environments male lobster’s nephropore gland is located so that it releases products into the urine. Urine is then injected into the gill current that jets water 1 to 2 meters ahead of the animal. This signal is sent out ahead of the lobster and dispersed quickly before the lobster arrives at location. Unlike in terrestrial environments where chemicals are dispersed through the air and at the mercy of winds, in marine environments chemical signals are quickly dispersed through diffusion and mass water flow (Atema 1995). Through this rapid and widespread dispersal organisms must be able to detect individual chemical signals from a potentially large array of other chemical signals given by any number of species of organisms. This would require receptor specificity as well as an ability to recognize timing and intensity of dispersal in order to distinguish between what is random and what is a true signal.
Mechanoreception

Tactile information may be obtained through direct touch or indirect seismic cues. Arthropod antennae are the main organs of tactile sensation though bristles on the cuticle are also used to sense vibration (Chidwari & Mercer 2003). Insects and crustaceans use their antennae for wall-following as well as obstacle detection (Camhi & Johnson 1999, Pelletier & McLeod 1994, Zeil et al. 1985.) Some cuticular structures also allow for orientation in the microtrich sensilla on the lotic amphipod *Gammarus pseudolimnaeus* Bousfield that enable it to control body orientation while swimming (Olyslager & Williams 1993).

Among insects the second segment of the antennae (the pedicel) contains the Johnston’s Organ. This organ detects motion in the flagellum (found on the third segment) and consists of over 200 scolopidia. The scolopidia each contain a mechanosensory chordotonal neuron that gathers information about texture, shape and orientation of objects (Yack 2004). The Johnston’s Organ has also been noted to detect wind as well as electric fields in bees. Bees emit constant and modulated electric fields when flying, landing, walking and during the waggle dance. Greggers et al. (2013) used recordings from axons of the Johnston organ to document its sensitivity to electric field stimuli coming from other bees.

In marine environments crustaceans react to mechanoreceptor stimulation much in the same way as terrestrial arthropods. Crayfish use their second antennae as well as their first to locate objects while walking. Zeil et al. (1985) used blind crayfish (*Cherax*
to test the sensitivity of mechanoreceptors to touch. They touched the antennae with a brush then recorded the direction taken and distance covered following the touch. There was a direct correlation between the direction and distance the crayfish covered and the angle at which the antenna is held during contact as well as the distance along the antennal flagellum at that the stimulus is applied.

Hearing

Arthropods that are capable of hearing possess tympanal organs that consist of a membrane stretched over a frame that is backed by an air sac. These tympanal ears are located in at least ten different regions in a diversity of insect taxa, for example; Lepidoptera; Sphingoidea, Orthoptera; Ensifera, and in Neuroptera; Chrysopidae (Fullard & Yack 1993). Moths of the super-family Noctuoidea for example have metathoracic tympanal ears that are used for the detection of echolocation calls of hunting bats. The ultrasound detectors of these moths are also used in courtship, female choice of mates, species recognition and male-male competition for females (Conner 1999). The tympanal ears even differ in complexity, for example notodontid moths have a single-celled ear whereas cicadas possess over 1,000 auditory neurons. The most common location for insect ears is the caudal thorax/rostral abdomen which is the location of 12 of the 19 known peripheral auditory systems. Other locations are on the legs, mesothorax, metathorax, various segments of the abdomen, wings and mouthparts (Yager 1999).

Auditory signals are important as they provide the opportunity of the receiver to gather input from a long range about the origins of the sender and its potential to be a threat. Sometimes long range is sufficient for an arthropod to recognize the signal as non-
threatening, but not as a conspecific. Male meadow katydids *Conocephalus nigropleurum* (Orthopera: Tettigoniidae) sing with gatherings of heterospecifics that obscures their song at long distances. Female *C. nigropleurum* seem to be attracted to any high frequency and do not recognize conspecifics until they are closer within the mixed species cluster (Gwynne & Morris 1986). Hearing can also be sexually dimorphic depending on the organism’s morphology or behavior. For example, male gypsy moths *Lymantria dispar* (Lepidoptera: Lymantriidae) have tympanal organs because they fly throughout the night and need to detect bat echolocation, females however do not have tympanal organs because they do not fly throughout the night.

The American cockroach *P. americana* detects sound in a very different way. A sense organ in the metathoracic legs is extremely responsive to vibration, but also detects sound with sensitivity similar to some insect tympanal organs. Although *P. americana* is thought to be deaf and appears to ignore loud tones presented to its colony small leg movements occur in response to sound confirming the presence of a functional auditory sense (Shaw 1994).

Auditory signals have effective range, ease of locating the source, and fast speed. The problem with reliance upon this signal is the persistence. The signal can only persist for as long as the sender can emit it. The receiver must be able to locate the origin of the sender before the sound is no longer emitted. If the persistence is short other signals may be required to efficiently locate and assess the sender.
**Predator avoidance strategies of arthropods**

When animals receive cues about predators they are not able to detect signals the predator has received about their location. Prey must then make the decision to flee or remain to detect additional information about the predator. The decision to flee may impact potential reproductive or feeding opportunities so the prey animal must evaluate the threat before reacting.

Some survival strategies are formed as morphological defenses in animals and not necessarily for avoidance at all. Certain species of woodlice in the genus *Armadillidium* for example have cuticles that are so impenetrable that a specific species of spider family, *Dysderidae*, have evolved extra large and powerful chelicerae that can puncture their armored cuticle (Rezáč et al. 2008). *Armadillidium* can also conglobate or roll into a protective ball when faced with predation.

Predators may be attracted to or repulsed by the armor content of prey before choosing their food source. The red-backed salamander (*Plethodon cinereus*) for instance evaluates the size and chitinous content of its arthropod prey due to the speed at which the prey moves through their digestive tracks. These salamanders feed on termites (Isoptera) and springtails (Collembola), that are lightly armored with chitinous exoskeletons, and ants (Hymenoptera: Formicidae) and beetles (Coleoptera), that are heavily armored with chitinous exoskeletons (Jaeger 1990). The passage time through the digestive tract is much faster for the dipterans (approximately 70 h) than for the ants (approximately 112 h) at 15°C (Jaeger & Bernard 1981). Jaeger (1990) showed that when foraging
opportunity was poor on dry days *P. cinereus* was less discriminate and ate both heavily and lightly armored prey in similar proportions, but when foraging on abundant wet days they were much more discriminate largely preferring lightly armored prey.

Arthropod prey react in specific ways to predatory threats. For example, when introduced to substrate previously exposed to the predatory spider *Hogna helluo* (Araneae: Lycosidae), the wolf spider and prey species *Pardosa milvina* (Araneae: Lycosidae) avoided the substrate more often than substrate not exposed to the predator (Persons et al. 2001). An aquatic insect called a back-swimmer, *Notonecta hoflrnatzni* (Hemiptera: Notonectidae) shows avoidance behavior towards predatory adult conspecifics. The juveniles change their foraging habits in the presence of adults, foraging in covered locations as well as less frequently (Sih 1982).

The Rove beetle, *Hypnogrya tubula* (Coleoptera: Staphylinidae), engages in a coiling up behavior when threatened. This behavior begins with the ventral part of the head pressing against the prosternum. The beetle then draws its legs inward, and finally coils its abdomen. This process takes only one second to complete once disturbed by tweezers (Yamazaki 2007). Other arthropods also engage in coiling up, such as millipedes, lepidopteran larvae and sawfly larvae. The pill bug, *Armadillidium vulgare*, completely conglobates into a protective sphere.

To initiate responses animals must be able to receive cues from the predator. These cues may be visual, tactile, chemical or auditory signals. Recognizing predatory threat may
require only one sensory modality or a combination of two or more before a response is initiated.

The present study addresses two questions: (1) how do cues with different sensory modalities affect frequency and average durations of prey action and (2) does action type and duration vary among different arthropod families? Due to different families evolving to adapt to varying environmental and behavioral pressures it would be expected they may react differently when in the presence of predators. In the present study, I investigate the actions of four arthropod species; *Blatella germanica* (Blattodea:Blattellidae), *Acheta domesticus* (Orthoptera:Gryllinae), *Armadillidium vulgare* (Oniscidea: Armadillidiidae), and *Porcellio laevis* (Oniscidea: Porcellionidae).

*Armadillidium vulgare* and *P. laevis* are primarily nocturnal terrestrial isopods found beneath leaf litter, other detritus and rocks. They are gregarious and regularly found in large numbers. Due to their initially evolving as marine organisms their evolutionary history as marine organisms led to the modification of gills into pleopodal lungs and are reliant upon humid terrestrial environments in order to survive (Hornung 2011).

Although distance responses to olfactory stimuli have not yet been demonstrated in this family of organisms, *Hemilepistus reaumuri* (Oniscidea: Trachelipodidae) specifically has been tested. The mixed olfactory-gustatory organ on the second antennae of terrestrial isopods seems to play an important role in social recognition, for group cohesion and for communication (Seelinger 1983, Linsenmair 2007). Due to these environmental and physiological limitations they would not be expected to rely on visual
ability, but more so upon chemical and seismic cues. They are also adapted to finding food through their chemoreceptors located in their antennae and have been recorded using odor of metabolites emitted by food colonizing microbiota to direct their food choice (Zimmer et al., 1996). This adaptation for foraging may also be applicable when sensing predatory threat.

*Acheta domesticus* are crepuscular to nocturnal crickets found in several different habitats such as urban environments, fields, and forests (Pinter 1972). These animals are not gregarious and rely upon auditory cues to make contact with conspecifics (Kiflawi & Gray 2000). The photoreceptors in compound eyes of nocturnal insects respond more slowly than diurnal photoreceptors that improve visual reliability in dim light. The narrower temporal bandwidth of nocturnal photoreceptors significantly reduces the inherent information rate. Their higher contrast gain provides beneficial signal amplification, but also amplifies the noise and leads to no improvement in the visual signal to-noise ratio (Warrant & Dacke 2011). Due to these issues with nocturnal vision I would expect visual cues to be important, but likely secondary to seismic cues. *Acheta domesticus* may be likely to respond to seismic cues due to their auditory sensitivity. Crickets have two tympanal membranes on the tibia of each foreleg that are used to receive auditory signals from potential mates (Mhatre et al 2009). Chemoreception may be less important as the role it plays in reproduction and mate finding requires contact to elicit a courtship response (Hardy & Shaw 1983). When used for predator detection it would be assumed contact or close proximity may be an important factor.
*Blatella germanica* are gregarious nocturnal cockroaches. Though *B. germanica* exhibit color discrimination, they are particularly sensitive to UV light (Koehler et al. 1987). Cockroach vision is mainly used to detect light change that causes scattering. These animals are nearly completely reliant upon tactile cues for all primary sensory input associated with social conditions. When studying rate of oocyte maturation and the effects of visual, chemical and tactile cues it was confirmed that *B. germanica* adult females require antennae alone to sufficiently receive stimuli that accelerate the reproductive cycle as well as triggering group effects in colonies (Uzsák & Schal 2013, Lihoreau & Rivault 2008). The antennae of cockroaches are complex sensory appendages that contain mechanoreceptors, chemoreceptors, thermoreceptors, hygroreceptors and several types of proprioceptors (Schaller 1978; Toh 1981; Toh and Yokohari 1985). It has been frequently documented that chemical communication is widely used in the *B. germanica* in many contexts including aggregation, long- and short-range mate attraction, courtship behavior leading to mate choice, and pre- and post-copulatory nuptial exchanges (Ishii & Kuwahara 1967, Wileyto et al. 1984, Dambach et al. 1994, Liang & Schal 1994, Norjima et al. 1999, Gemeno & Schal 2004, Norjima et al. 2005, Eliyahu et al. 2008). Blatellids rely heavily on their antennae for receiving cues so it would be expected cues connected to these structures would be important in driving behavior. It would therefore be expected then that seismic and chemical cues in this experiment would be of primary importance when assessing predatory threat.
Material and Methods

Experimental Animals

The animals used in these experiments were purchased from Carolina Biological (http://www.carolina.com) and Todd Gearheart (http://www.tarantulaspiders.com) All organisms were wild caught (except A.domesticus) in North Carolina and Florida respectively. Pill bugs, A. vulgare, and sow bugs, P. laevis, were housed in the cardboard containers they were shipped in and periodically misted with water to maintain adequate humidity levels. The house crickets, A. domesticus, were kept in a 38L glass aquarium and fed commercial cricket food ad libitum. The German cockroaches, B. germanica, were kept in a plastic pet container (Pet Keeper™) with a cardboard refuge tube and fed Taste of the Wild™ dry cat food ad libitum. All experimental predators, Wolf spiders and Six-spotted fishing spiders, Dolomedes triton, were housed in the individual plastic containers they were shipped in. The containers were kept appropriately humid with a damp paper towel, had a small container of water and the spiders were fed one to two crickets a week on the same day every week.

Prey animals were chosen at random for each trial and their length was recorded. The age of both predator and prey were unknown. The predatory spiders were chosen the morning of the experiment and used throughout each trial until signs of stress were apparent (i.e. low crouching near the edge of the arena walls without movement for several trials) in that case they were exchanged for a different spider. The exception to this was D. triton that never required replacement as it is their normal behavior to remain in a stationary position. In the event that a spider perished, it was replaced in the laboratory population
with a novel spider. Each spider was given a number for identification that was recorded along with its size, sex and species. Due to the biological supply company supplying diverse specimens six species of wolf spiders were used as predators; *Hogna lenta*, *Hogna antelucana*, *Hogna carolinensis*, *Tygrosa annexa* and *Rabidosa rabida* (Aranea: Lycosidae), and *Dolomedes triton* (Araneae: Pisauridae).

**Experimental Design**

Eight experiments were run for two minutes per trial, with twenty trials per prey animal; fifteen using Lycosids as the predator and five using *D. triton* (Table 1). All cues were tested alone, in combination with another cue and all three together as well as without a barrier. Between each trial the substrate was cleaned with 70% alcohol to eliminate any chemical cues left from the previous trial. To assess predator avoidance behavior the frequency and durations of relevant behavioral patterns (Table 2) were recorded using the Noldus Observer™ 2.0 event recording software.

**Behaviors**

The frequencies per trial and average durations of several common behaviors were recorded for each prey species; walking, running, stasis and antennal movement. The difference between walking and running behaviors were discrete. It was assumed all four species exhibit these behaviors in their natural environments and would change these behaviors when presented with a predatory threat. Locomotion may change in frequency and durations while either avoiding or escaping a predator. It was also assumed antennal movement may change as the prey animals search for chemical cues received from their environment and potential threats. Antennal movement is also important in *B. germanica*
when navigating its environment and searching for obstructions and therefore may change when faced with a predator. There are also species specific protective behavior that may change in the presence of a predator; conglobation for *A. vulgare* and hopping for *A. domesticus*, and may be completely reliant upon predator contact.

**Apparatus Design**

All trials took place within an arena (Figure 1) built using 22cm diameter aluminum flashing fashioned into a cylinder wrapped in paper to prevent animals from escaping underneath the wall; the sides were coated with Vaseline™ petroleum jelly to prevent escape, especially by *B. germanica* that could readily climb walls. A 7cm diameter cylinder constructed from a clear overhead transparency sheet containing the prey animal was placed in the center with 15cm of space between it and the flashing (Figure 1). For all experiments and trials, before the beginning of each trial a predatory spider was placed beneath a 7cm diameter aluminum covering attached to a string. Once the trial began the prey was allowed approximately 15-20 seconds alone in the arena for baseline observations without a predator present. At the end of the 15 to 20 seconds acclimation period the string was retracted to remove the aluminum covering, allowing the predator access to the arena outside the plastic cylinder. The same procedure was followed during the control. All actions from both predator and prey were then recorded until the end of the trial at 120 seconds.

**Seismic Cues**

Trials including seismic cues (S+) took place within the aluminum arena upon a 33cm diameter snare drum (Pulse Piccolo) where all seismic activity was then recorded using
the program Audacity™ via an electric piezo transducer (Cherub WCP-60) that detected and transmitted data to a laptop. Trials not involving the assessment of seismic cues (S-) were conducted upon the drumhead removed from the drum and laid upon a vibration dampening mat, with the aluminum flashing arena surrounding the animals.

**Visual Cues**

All trials including visual cues (V+) took place within a clear transparency sheet taped into a cylinder. Trials excluding visual cues (V-) took place within a clear transparency sheet taped into a cylinder that was blacked out with a Sharpie™ marker, where the cylinder was allowed 24 hours to dry and dissipate solvent odors.

**Chemical Cues**

Trials including chemical cues moving through the apparatus (C+) took place within the cylinder that had previously had <5mm holes punched into it as well as 5mm wide slits cut above line of sight for all subjects that ran the length of the cylinder. The holes and slits were cut with a sterilized probe and scissor respectively. Trials excluding chemical cues (C-) took place within the cylinder without holes or slits.

**Experiment 1: Visual (+), Seismic (-) and Chemical (-).** Each V+/S-/C- trial began with the prey animal within the clear transparency sheet cylinder in the center of the arena. The substrate was the drumhead removed from the drum and placed upon the vibration dampening mat.
Experiment 2: Chemical (+), Visual (-) and Seismic (-). Each C+/V-/S- trial began with the prey animal within the blacked out transparency sheet cylinder with holes and slits cut into it. The substrate was the drumhead removed from the drum and placed upon the vibration dampening mat.

Experiment 3: Seismic (+), Visual (-) and Chemical (-). Each S+/V-/C- trial began with the prey animal within the blacked out transparency sheet cylinder with holes and slits cut into it. The substrate was the unaltered snare drum.

Experiment 4: Visual (+) and Chemical (+), Seismic (-). Each V+/C+/S- trial began with the prey animal within the clear transparency sheet cylinder with holes and slits cut into it, in the center of the arena. The substrate was the drumhead removed from the drum and placed upon the vibration dampening mat.

Experiment 5: Visual (+) and Seismic (+), Chemical (-). Each V+/S+/C- trial began with the prey animal within the clear transparency sheet cylinder in the center of the arena. The substrate was the unaltered snare drum.

Experiment 6: Chemical (+) and Seismic (+), Visual (-). Each C+/S+/V- trial began with the prey animal within the blacked out transparency sheet cylinder with holes and slits cut into it. The substrate was the unaltered snare drum.
Experiment 7: Visual (+), Chemical (+) and Seismic Cues (+). Each V+/C+/S+ trial began with the prey animal within the clear transparency sheet cylinder with holes and slits cut into it in the center of the arena. The substrate was the unaltered snare drum.

Experiment 8: Control. Each V+/C+/S+ trial began without any transparency sheet cylinder. The substrate was the unaltered snare drum.

Experiment 9: V+/C+/S+ No Barrier

The trials that tested for prey reaction to visual, chemical and seismic cues from the predator without barriers were run in order to control for possible prey reaction being influenced by a barrier. Removing barriers allows the predator and prey physical contact that may cause different responses from the prey animal than when no physical contact or predation was possible. It is also possible the transparency sheet could contain chemical properties or not allow enough flow of chemical cues through the holes made in it and may skew results. There is potential as well for visual cues to be skewed through the transparency sheet depending on the prey animal’s visual morphology.

Results

Statistical analyses were conducted on the frequency and average durations of each behavior within each treatment. Behavior between species was compared and statistically analyzed using an analysis of variance (ANOVA) with Tukey’s post hoc test while behavior within species was compared with conspecific controls and statistically analyzed with the Student T-test for Two Samples. Statistical significance was
determined with $\alpha = 0.05$, although analyses with multiple comparisons may be more conservatively evaluated with a Bonferroni-corrected $\alpha$ value of 0.0125.

**Visual (+), Seismic (-), Chemical (-)**

A summary of statistical comparisons between treatment and control groups for each species can be found in Table 4 and Table 5.

**Walking**

In *P. laevis*, treatment animals exhibited significantly higher frequencies of walking than control conspecific animals (Figure 4, T-Test, $T = -1.83$, $p = 0.0375$). Average durations of walking behavior in control *P. laevis* and control *A. domesticus* were significantly higher than conspecific treatment animals (Figure 5, T-Test, $T = 3.19$, $p = 0.0014$ and $T = 3$, $p = 0.0023$, respectively).

The frequency of walking behavior was significantly higher in *A. domesticus* than in *A. vulgar* and *B. germanica* (Figure 2, ANOVA, $F(3, 76)=4.21$, $p = 0.0082$). The average durations of walking behavior was significantly higher in *A. domesticus* than in the other three animals (Figure 3, ANOVA, $F(3, 76)= 8.57$, $p = <0.0001$).

**Antennal Movement**

The frequency of antennal movement was significantly higher in *A. domesticus* than all three other species (Figure 2, ANOVA, $F(3, 76)=23.40$, $p <0.0001$). The average
durations of antennal movement behavior of *A. vulgare* was significantly higher than *B. germanica* (Figure 3, ANOVA, F(3, 76)=5.93, p= 0.0010)

In *A. vulgare* treatment animals exhibited significantly higher frequencies of antennal movement than conspecific control animals. In *A. domesticus* and *B. germanica* control animals exhibited significantly higher frequencies of antennal movement than treatment conspecific animals. (Figure 6, T-test, T= -4.93, p= <0.0001, T= -3.83, p=0.0002 and T=1.99, p=0.027, respectively). In *A. vulgare* and *P. laevis*, treatment animals exhibited significantly higher average durations of antennal movement than conspecific control animals (Figure 7, T-Test, T = -3.77, p = 0.0002 and T = -3.98, p = 0.0001, respectively).

**Running**

There were no significant differences between species or between test treatment and control or within species for running frequency and average durations.

**Stasis**

The frequency of stasis behavior was significantly higher in *A. domesticus* than all three other species (Figure 2, ANOVA, F(3, 76)=25.74, p <0.0001). There were no significant differences between species for stasis average durations.

In *A. vulgare*, *P. laevis* and *A. domesticus*, treatment animals exhibited significantly higher frequencies of stasis behavior than conspecific control animals (Figure 8, T-test,
T= -1.61, p=0.0585, T= -4.73, p <.0001, and T= -3.39, p = 0.0008, respectively). There were no significant differences within species for stasis average durations.

Climbing

There were no significant differences between species or between test treatment and control or within species for frequency and average durations of climbing behavior.

Grooming

The frequency of grooming behavior was significantly higher in *A. domesticus* than all three other species (Figure 2, ANOVA, F(3, 76)=4.13, p = 0.0090). There were no significant differences between species for average durations of stasis behavior.

There were no significant differences within species for frequency or average durations of stasis behavior.

**Chemical (+), Visual (-), Seismic (-)**

A summary of statistical comparisons between treatment and control groups for each species can be found in Table 6 and Table 7.

Walking

There were no significant differences between species for frequency of walking behavior. The average durations of walking behavior was significantly higher in *A. vulgare* and *P. laevis* than in *A. domesticus* (Figure 10, ANOVA, F(3, 76)= 7.08, p= 0002).
There were no significant differences within species for frequency or average durations of walking behavior.

**Antennal Movement**

The frequency of antennal movement behavior in *A. domesticus* was significantly higher than in all three other species. Frequency of antennal movement behavior was also significantly higher in *B. germanica* than in *P. laevis* (Figure 9, ANOVA, F(3, 76)= 44.62, p <0.0001). The average durations of antennal movement behavior was significantly higher in *A. domesticus* than in all three other species as well as in *B. germanica* than in *P. laevis* (Figure 10, ANOVA, F(3, 76)= 16.31, p <0.0001).

In *A. vulgare* and *A. domesticus*, treatment animals exhibited significantly higher frequencies of antennal movement than in conspecific control animals (Figure 11, T-test, T= -2.08, p=0.0221 and T= -4.83, p= 0.0239, respectively). In *A. domesticus*, treatment animals exhibited significantly higher frequencies of antennal movement than in conspecific control animals (Figure 12, T-test, T= -4.17, p <0.0001).

**Running**

There were no significant differences between species or within species for frequency and average durations of climbing behavior.
Stasis

The frequency of stasis behavior was significantly higher in *A. domesticus* than all three other species (Figure 9, ANOVA, F(3, 76)=40.59, p <0.0001). There were no significant differences between species or within species for stasis average durations.

In *A. domesticus*, treatment animals exhibited significantly higher frequencies of stasis behavior than in conspecific control animals (Figure 13, T-test, T= -4.3, p= 0.0001). There were no significant differences within species of average durations of stasis behavior.

Climbing

There were no significant differences between species or within species for frequency and average durations of climbing behavior.

Grooming

The frequency of grooming behavior was significantly higher in *A. domesticus* than all three other species (Figure 9, ANOVA, F(3, 76)= 7.95, p= 0.0001). The average durations of grooming behavior was significantly higher in *A. domesticus* than in all three other species (Figure 10, ANOVA, F(3, 76)= 15.39, p <0.0001).

In *A. domesticus*, treatment animals exhibited significantly higher frequencies of grooming behavior than in conspecific control animals (Figure 14, T-test, T= -2.37, p= 0.0011). There were no significant differences within species of average durations of grooming behavior.
Seismic (+), Visual (-), Chemical (-)

A summary of statistical comparisons between treatment and control groups for each species can be found in Table 8 and Table 9.

Walking

The frequency of walking behavior was significantly higher in *P. laevis* and *A. vulgare* than *B. germanica* and higher in *A. domesticus* than all three other species (Figure 15, ANOVA, $F(3, 76)= 15.44$, $p<0.0001$). The average durations of walking behavior was significantly higher in *A. vulgare* and *P. laevis* than both *A. domesticus* and *B. germanica* (Figure 16, ANOVA, $F(3, 76)= 12.24$, $p>0.0001$).

In *P. laevis* and *A. domesticus* treatment animals exhibited significantly higher frequencies of walking behavior than in conspecific animals. In *B. germanica* control animals exhibited significantly higher frequencies of walking behavior than in treatment animals. (Figure 17, T-test, $T= -1.84$, $p=0.0367$, $T= -4.67$, $p<0.0001$, and $T= 3.94$, $p=0.0001$, respectively). In *A. vulgare*, *P. laevis*, *A. domesticus* and *B. germanica* control animals exhibited significantly higher average durations of walking behavior than in conspecific treatment animals (Figure 18, T-test, $T= 1.94$, $p=0.0299$, $T= 2.88$, $p=0.0032$, $T= 3.03$, $p=0.0021$, and $T= 3.76$, $p=0.0002$, respectively).
Antennal Movement

The frequency of antennal movement behavior was significantly higher in *A. domesticus* than all three other species (Figure 15, ANOVA, \(F(3, 76)= 20.61, p<0.0001\)). The average durations of antennal movement behavior was significantly higher in *B. germanica* than *A. domesticus* (Figure 16, ANOVA, \(F(3, 76)= 3.22, p= 0.0273\)).

In *A. vulgare, P. laevis, A. domesticus* and *B. germanica* treatment animals exhibited significantly higher frequencies of antennal movement than in conspecific control animals (Figure 19, T-test, \(T= -5.76, p<0.0001, T= -4.05, p= 0.0001, T= -5.32, p<0.0001,\) and \(T= -4.67, p<0.0001,\) respectively). In *A. vulgare, P. laevis, and B. germanica* treatment animals exhibited significantly higher average durations of antennal movement than in conspecific control animals (Figure 20, T-test, \(T= -4.18, p<0.0001, T= -4.10, p= 0.0001,\) and \(T= -6.22, p<0.0001\)).

Running

There were no significant differences between species or within species for frequency and average durations of running behavior.

Stasis

The frequency of stasis behavior was significantly higher in *A. domesticus* and *B. germanica* than in both *A. vulgare* and *P. laevis* (Figure 15, ANOVA, \(F(3, 76)= 16.63, p<.0001\)). There were no significant differences between species average durations of stasis behavior.
In *A. domesticus* and *B. germanica* treatment animals exhibited significantly higher frequencies of stasis behavior than in conspecific control animals (Figure 21, T-test, T = -2.13, p = 0.0132 and F(3, 76) = -3.98, p = 0.0001). There were no significant differences within species for average durations of stasis behavior.

**Climbing**

The frequency of climbing behavior was significantly higher in *B. germanica* than in all three other species (Figure 15, ANOVA, F(3, 76) = 5.38, p = 0.0020). There were no significant differences between species average durations of climbing behavior.

There were no significant differences within species for frequency and average durations of climbing behavior.

**Grooming**

There were no significant differences between species for frequency of grooming behavior. The average durations of grooming behavior was significantly higher in *B. germanica* than in all three other species (Figure 16, ANOVA, F(3, 76) = 4.62, p = 0.0050).

There were no significant differences within species for frequency of grooming behavior. In *A. domesticus* control animals exhibited significantly higher average durations of grooming behavior than in conspecific treatment animals (Figure 22, T-test, T = 2.11, p = 0.0207). In *B. germanica* treatment animals exhibited significantly higher average
durations of grooming behavior than in conspecific control animals (Figure 22, T-test, T= -1.71, p= 0.0477).

**Visual (+), Chemical (+), Seismic (-)**

A summary of statistical comparisons between treatment and control groups for each species can be found in Table 10 and Table 11.

**Walking**

There were no significant differences between species for frequency of walking behavior. The average durations of walking behavior was significantly higher in *P. laevis* and *B. germanica* than in *A. domesticus* (Figure 23, ANOVA, F(3, 76)= 4.25, p= 0.0078).

There were no significant differences within species for frequency of walking behavior. In *A. vulgare*, *P. laevis*, and *A. domesticus* control animals exhibited significantly higher average durations of walking behavior than in conspecific treatment animals (Figure 24, T-test, T= 2.14, p= 0.020, T= 2.20, p= 0.0170, and T= 2.63, p= 0.0080, respectively).

**Antennal Movement**

There were no significant differences between species for frequency and average durations of antennal movement.

In *A. vulgare*, *P. laevis*, *A. domesticus* and *B. germanica* treatment animals exhibited significantly higher frequencies of antennal movement than in conspecific control
animals (Figure 25, T-test, T= -5.72, p < 0.0001, T= -3.50, p= 0.0006, T= -3.05, p= 0.0021, and T= -2.16, p= 0.0196, respectively). In *A. vulgare, P. laevis, A. domesticus* and *B. germanica* treatment animals exhibited significantly higher average durations of antennal movement than in conspecific control animals (Figure 26, T-test, T= -5.64, p < 0.0001, T= -5.12, p= 0.0001, T= -2.79, p= 0.0042, and T= -2.99, p= 0.0029, respectively).

**Running**

There were no significant differences between species or within species for frequency and average durations of running behavior.

**Stasis**

The frequency of stasis behavior was significantly higher in *A. domesticus* than in all three other species (Figure 23, ANOVA, F(3, 76)= 16.29, p < 0.0001). There were no significant differences between species for average durations of stasis behavior.

In *P. laevis* and *A. domesticus* treatment animals exhibited significantly higher frequency of stasis behavior than in conspecific control animals (Figure 27, T-test, T= -2.39, p= 0.013 and T= -2.79, p= 0.0004, respectively). There were no significant differences within species for average durations of stasis behavior.

**Climbing**

This behavior did not occur in any species.

**Grooming**
This behavior did not occur in any species.

**Visual (+), Seismic (+), Chemical (-)**

A summary of statistical comparisons between treatment and control groups for each species can be found in Table 12 and Table 13.

**Walking**

There were no significant differences between species for frequency of walking behavior. The average durations of walking behavior was significantly higher in *A. vulgare* than in *A. domesticus* and *B. germanica* (Figure 33, ANOVA, F(3, 76)= 5.35, p= 0.0021).

In *A. vulgare*, *P. laevis*, *A. domesticus* and *B. germanica* treatment animals exhibited significantly higher frequencies of walking behavior than in conspecific control animals (Figure 29, T-test, T= -2.66, p= 0.00056, T= -3.32, p= 0.0009, T= -1.81, p= 0.0391, and T= -1.79, p= 0.040, respectively). In *A. vulgare*, *P. laevis*, *A. domesticus* and *B. germanica* control animals exhibited significantly higher average durations of walking behavior than in conspecific treatment animals (Figure 30, T-test, T= 2.04, p= 0.0241, T= 4.15, p <0.0001, T= 2.42, p= 0.0102, and T= 3.25, p= 0.0012, respectively).

**Antennal Movement**

The frequency of antennal movement was significantly higher in *A. domesticus* than in *A. vulgare* and *P. laevis*. The frequency of antennal movement was significantly higher in *B.
germanica than in P. laevis and A. domesticus (Figure 28, ANOVA, F(3, 76)= 11.30, p <0.0001). There were no significant differences between species for average durations of antennal movement behavior.

In A. vulgare, P. laevis, A. domesticus and B. germanica treatment animals exhibited significantly higher frequencies of antennal movement than in conspecific control animals (Figure 31, T-test, T= -3.02, p= 0.0022, T= -2.07, p= 0.0226, T= -3.36, p= 0.0008, and T= -4.72, p <0.0001, respectively). In A. vulgare, P. laevis, A. domesticus and B. germanica treatment animals exhibited significantly higher average durations of antennal movement than in conspecific control animals (Figure 32, T-test, T= -3.20, p= 0.0013, T= -3.20, p= 0.0013, T= -3.89, p= 0.0001, and T= -3.46, p= 0.0006, respectively).

**Running**

There were no significant differences between species or within species for frequency and average durations of running behavior.

**Stasis**

The frequency of stasis behavior was significantly higher in A. domesticus than in all three other species (Figure 28, ANOVA, F(3, 76)= 6.52, p= 0.0005). The average durations of stasis behavior was significantly higher in A. domesticus than in A. vulgare (Figure 33, ANOVA, F(3, 76)= 3.09, p= 0.032).
In *A. domesticus* treatment animals exhibited significantly higher frequencies of stasis behavior than in conspecific control animals (Figure 34, T-test, $T = -1.86$, $p = 0.0358$). There were no significant differences within species for average durations of stasis behavior.

**Climbing**

The frequency of climbing behavior was significantly higher in *B. germanica* than in all three other species (Figure 28, ANOVA, $F(3, 76)= 9.22$, $p < 0.0001$). The average durations of climbing behavior was significantly higher in *B. germanica* than in all three other species (Figure 33, ANOVA, $F(3, 76)= 9.46$, $p < 0.0001$).

There were no significant differences within species for frequency and average durations of climbing behavior.

**Grooming**

The frequency of grooming behavior was significantly higher in *A. domesticus* than in all three other species (Figure 28, ANOVA, $F(3, 76)= 3.88$, $p = 0.0122$). The average durations of grooming behavior was significantly higher in *A. domesticus* than in all three other species (Figure 33, ANOVA, $F(3, 76)= 4.53$, $p = 0.0056$).

There were no significant differences within species for frequency and average durations of grooming behavior.
**Chemical (+), Seismic (+), Visual (-)**

A summary of statistical comparisons between treatment and control groups for each species can be found in Table 14 and Table 15.

**Walking**

There were no significant differences between species for frequency of walking behavior. The average durations of walking behavior was significantly higher in *A. vulgare* and *P. laevis* than in *A. domesticus* and *B. germanica* (Figure 35, ANOVA, $F(3, 76)= 31.48$, $p < 0.0001$).

In *B. germanica* control animals exhibited significantly higher frequencies of walking behavior than in conspecific treatment animals (Figure 37, T-test, $T= 1.90$, $p= 0.0325$). In *A. vulgare, P. laevis, A. domesticus* and *B. germanica* control animals exhibited significantly higher average durations of walking behavior than in conspecific treatment animals (Figure 38, T-test, $T= 3.57$, $p= 0.0004$).

**Antennal Movement**

The frequency of antennal movement behavior was significantly higher in *A. domesticus* than in all three other species. The frequency of antennal movement behavior was significantly higher in *B. germanica* than in *P. laevis* (Figure 35, ANOVA, $F(3, 76)= 16.89$, $p < 0.0001$). The average durations of antennal movement behavior was significantly higher in *B. germanica* than in all three other species (Figure 36, ANOVA, $F(3, 76)= 12.36$, $p < 0.0001$).
In *A. vulgare, P. laevis, A. domesticus* and *B. germanica* treatment animals exhibited significantly higher frequencies of antennal movement than in conspecific control animals (Figure 39, T-test, $T= -7.88$, $p <0.0001$, $T= -3.63$, $p= 0.0004$, $T= -5.31$, $p <0.0001$, and $T= -4.89$, $p <0.0001$, respectively). In *A. vulgare, P. laevis, A. domesticus* and *B. germanica* treatment animals exhibited significantly higher average durations of antennal movement than in conspecific control animals (Figure 40, T-test, $T= -4.63$, $p <0.0001$, $T= -3.52$, $p= 0.0005$, $T= -4.49$, $p <0.0001$, and $T= -5.79$, $p <0.0001$, respectively).

**Running**

There were no significant differences between species or within species for frequency and average durations of running behavior.

**Stasis**

The frequency of stasis behavior was significantly higher in *A. domesticus* than in all three other species (Figure 35, ANOVA, $F(3, 76)= 16.65$, $p <0.0001$). The average durations of stasis behavior was significantly higher in *A. domesticus* and *B. germanica* than in *P. laevis* (Figure 36, ANOVA, $F(3, 76)= 4.27$, $p= 0.0076$).

In *P. laevis* control animals exhibited significantly higher frequencies of stasis behavior than in conspecific treatment animals. In *A. domesticus* treatment animals exhibited significantly higher frequencies of stasis behavior than in conspecific control animals. (Figure 41, T-test, $T= 1.86$, $p= 0.0353$ and $T= -1.96$, $p= 0.0286$, respectively). In *B.*
germanica treatment animals exhibited significantly higher average durations of stasis behavior than in conspecific control animals (Figure 42, T-test, T= -2.08, p= 0.0221).

Climbing and Grooming

There were no significant differences between species or within species in the frequency or average durations of climbing behavior. This was also the case for grooming behavior.

Visual (+), Chemical (+), Seismic (+)

A summary of statistical comparisons between treatment and control groups for each species can be found in Table 16 and Table 17.

Walking

The frequency of walking behavior was significantly higher in P. laevis than in B. germanica (Figure 43, ANOVA, F(3, 76)= 3.28, p= 0.0254). The average durations of walking behavior was significantly higher in A. vulgare and P. laevis than in A. domesticus and B. germanica (Figure 44, ANOVA, F(3, 76)= 14.56, p <0.0001).

In B. germanica control animals exhibited significantly higher frequencies of walking behavior than in conspecific treatment animals (Figure 45, T-test, T= 3.77, p= 0.0002). In A. vulgare, P. laevis, A. domesticus and B. germanica control animals exhibited significantly higher average durations of walking behavior than in conspecific treatment animals (Figure 46, T-test, T= 2.53, p= 0.0078, T= 3.68, p= 0.0003, T= 3.29, p= 0.0010 and T=3.47, p= 0.0006, respectively).
**Antennal Movement**

The frequency of antennal movement was significantly higher in *A. domesticus* than in *A. vulgare* and *P. laevis*. The frequency of antennal movement was significantly higher in *B. germanica* than in *A. vulgare* (Figure 43, ANOVA, F(3, 76) = 7.04, p = 0.0003). The average durations of antennal movement behavior was significantly higher in *A. domesticus* than in *A. vulgare* and *P. laevis* (Figure 44, ANOVA, F(3, 76) = 5.35, p = 0.0021).

There were no significant differences within species for frequency and average durations of grooming behavior.

**Running**

There were no significant differences between species or within species for frequency and average durations of running behavior.

**Stasis**

The frequency of stasis behavior was significantly higher in *A. domesticus* than in all three other species (Figure 43, ANOVA, F(3, 76) = 12.31, p <0.0001). There were no significant differences between species for average durations of stasis behavior.

In *A. vulgare, P. laevis, A. domesticus* and *B. germanica* treatment animals exhibited significantly higher frequencies of stasis behavior than in conspecific control animals (Figure 47, T-test, T = -0.25, p = 0.0144, T = -4.62, p <0.0001, T = -2.55, p = 0.0074, and T =
-1.79, p = 0.040, respectively). In *A. domesticus* and *B. germanica* treatment animals exhibited significantly higher average durations of stasis behavior than in conspecific control animals (Figure 48, T-test, T = -2.21, p = 0.0166 and T = -1.86, p = 0.0353).

**Climbing**

There were no significant differences between species for frequency and average durations of climbing behavior.

In *B. germanica* control animals exhibited significantly higher frequencies of climbing behavior than in conspecific treatment animals (Figure 49, T-test, T = 1.67, p = 0.0515). In *B. germanica* control animals exhibited significantly higher average durations of climbing behavior than in conspecific treatment animals (Figure 50, T-test, T = 1.83, p = 0.0375).

**Grooming**

The frequency of grooming behavior was significantly higher in *B. germanica* than in all three other species (Figure 43, ANOVA, F(3, 76) = 6.05, p = 0.0009). The average durations of grooming behavior was significantly higher in *B. germanica* than in all three other species (Figure 44, ANOVA, F(3, 76) = 5.34, p = 0.0021).

In *B. germanica* control animals exhibited significantly higher frequencies of grooming behavior than in conspecific treatment animals (Figure 50, T-test, T = -2.23, p = 0.0158). In *B. germanica* treatment animals exhibited significantly higher average durations of
grooming behavior than in conspecific control animals (Figure 51, T-test, T = -1.69, p = 0.0496).

**Visual (+), Chemical (+), Seismic (+) No Barrier**

A summary of statistical comparisons between treatment and control groups for each species can be found in Table 18 and Table 19.

**Walking**

There were no significant differences between species for frequency and average durations of walking behavior.

In *A. vulgare, P. laevis* and *A. domesticus* treatment animals exhibited significantly higher frequencies of walking behavior than in conspecific control animals (Figure 54, T-test, T = -2.01, p = 0.0273, T = -2.41, p = 0.010, and T = -1.96, p = 0.030, respectively). In *A. vulgare, P. laevis* and *B. germanica* control animals exhibited significantly higher average durations of walking behavior than in conspecific treatment animals (Figure 55, T-test, T = 1.93, p = 0.0314, T = 2.75, p = 0.0047, and T = 3.23, p = 0.0018, respectively).

**Antennal Movement**

The frequency of antennal movement was significantly higher in *A. domesticus* than in all three other species. The frequency of antennal movement behavior was significantly higher in *B. germanica* than in *A. vulgare* (Figure 53, ANOVA, F(3, 76) = 16.03, p
<0.0001). There were no significant differences between species for average durations of antennal movement behavior.

In *A. vulgare*, *P. laevis*, *A. domesticus*, and *B. germanica* treatment animals exhibited significantly higher frequencies of antennal movement than in conspecific control animals (Figure 56, T-test, $T= -5.01, p <0.0001$, $T= -3.94, p= 0.0002$, $T= -5.21, p <0.0001$, and $T= -5.67, p <0.0001$, respectively). In *A. vulgare*, *P. laevis*, *A. domesticus*, and *B. germanica* treatment animals exhibited significantly higher average durations of antennal movement than in conspecific control animals (Figure 57, T-test, $T= -4.54, p <0.0001$, $T= -2.78, p= 0.0059$, $T= -1.65, p= 0.0581$, and $T= -5.02, p <0.0001$, respectively).

**Running**

The frequency of running behavior was significantly higher in *A. domesticus* than in *A. vulgare* (Figure 53, ANOVA, $F(3, 76)= 3.08, 0.0324$). There were no significant differences between species for average durations of walking behavior.

In *A. domesticus* and *B. germanica* treatment animals exhibited significantly higher frequencies of running behavior than in conspecific control animals (Figure 58, T-test, $T= -1.89, p= 0.0368$, and $T= -1.83, p= 0.0414$, respectively). In *A. domesticus* treatment animals exhibited significantly higher average durations of running behavior than in conspecific control animals (Figure 59, T-test, $T= -2.15, p= 0.0221$).
Stasis

The frequency of stasis behavior was significantly higher in *A. domesticus* than in all three other species. The frequency of stasis behavior was significantly higher in *P. laevis* than in *A. vulgare* (Figure 53, ANOVA, F(3, 76)= 27.04, p <0.0001). There were no significant differences between species for average durations of stasis behavior.

In *P. laevis* and *A. domesticus* treatment animals exhibited significantly higher frequencies of stasis behavior than in conspecific control animals (Figure 60, T-test, T= -2.72, p= 0.0056 and T= -2.96, p= 0.0027). There were no significant differences within species for average durations of stasis behavior.

Climbing

No climbing behavior occurred.

Grooming

The frequency of grooming behavior was significantly higher in *A. domesticus* than in *A. vulgare* and *P. laevis* (Figure 53, ANOVA, F(3,6)= 5.98, p=0.0010). There were no significant differences between species for average durations of grooming behavior.

There were no significant differences within species for frequency and average durations of grooming behavior.

Conglobation

Conglobation only occurred once in *A. vulgare*. 
Hopping

In *A. domesticus* treatment animals the frequency of hopping behavior was significantly higher than in conspecific control animals (Figure 61, T-test, T= -1.98, p= 0.0310).

Control

Walking

There were no significant differences between species for frequency of walking behavior. The average durations of walking behavior was significantly higher in *P. laevis* than in *A. domesticus* (Figure 63, ANOVA, F(3, 76)= 3.32, p= 0.0241).

Antennal Movement

The frequency of antennal movement was significantly higher in *A. domesticus* than in *A. vulgare* and *P. laevis*. The frequency of antennal movement was also significantly higher in *B. germanica* than in *P. laevis* and *A. vulgare* (Figure 62, ANOVA, F(3, 76)= 7.04, p= 0.0003). The average durations of antennal movement was significantly higher in *A. domesticus* than in *A. vulgare* and *P. laevis*. (Figure 63, ANOVA, F(3,76)= 5.34, p=0.0021).

Running

There were no significant differences between species or within species for frequency and average durations of running behavior.
Stasis

The frequency of stasis behavior was significantly higher in *A. domesticus* than in all three other species (Figure 62, ANOVA, F(3, 76)= 7.53, p= 0.0001). There were no significant differences between species for average durations of stasis behavior.

Climbing

The frequency of climbing behavior was significantly higher in *A. domesticus* than in all three other species (Figure 62, ANOVA, F=(3, 76)= 5.38, p= 0.0020). The average durations of climbing behavior was significantly higher in *B. germanica* than in all three other species (Figure 63, ANOVA, F=(3, 76)= 10.37, p<0.0001).

Grooming

The frequency of grooming behavior was significantly higher in *A. domesticus* than in *A. vulgare* and *P. laevis* (Figure 62, ANOVA, F(3, 76)= 4.58, p = 0.0053). The average durations of grooming behavior was significantly higher in *A. domesticus* than in all three other species (Figure 63, ANOVA, F(3, 76)= 5.04, p= 0.0030).

Discussion

Sensory cues influence the movements and actions made by prey animals. The prey animals in this study reacted differently depending on which cues they received as well as which prey species was the receiver.
Visual Cues

Visual cues are likely to be more salient for diurnal animals than for crepuscular or nocturnal animals or those inhabiting other low to no light environments. Species that evolved in dark or low-light environments would be expected to rely more upon chemical or seismic cues when exhibiting reaction to predatory threats. The animals in this study all inhabit low light to no light environments and would be expected to not rely heavily on visual cues.

This expectation was supported as for most trials treatment animals did not exhibit higher frequencies or average durations of behaviors over control conspecifics when exposed to only visual cues (V+/C-/S-) and when they did it was only for antennal movement and stasis behaviors. Antennal movement behavior was higher in at least a few treatment animal species per experiment than conspecific control animals (other than V+/C+/S+) signifying that perhaps this behavior is not limited by the receiving or denying of any cues or the prey animals may be searching for chemical cues they are not receiving. Due to the expected heavy reliance upon tactile and chemical cues in all four species it would not be unusual for frequent antennal movement regardless of cues received. This would especially be expected and was represented in B. germanica due to their reliance upon tactile information (Lihoreau & Rivault 2008). Stasis behavior was higher in at least a few treatment animal species per experiment than control conspecific animals as well, also signifying frequency and average durations of stasis behavior may not be dependent upon receiving or denying of cues. Stasis behavior frequency and average durations not dependent upon cues received may be due to the animals pausing in their movements in
order to realign their bodies in a position to better receive cues or to pause if they do not detect a threat.

**Chemical Cues**

Chemical cues are likely to be more important to animals that are nocturnal or live in low light environments, but also for animals that do receive visual cues. Because visual cues are not always possible even in well-lit environments animals that are capable of receiving them will also rely upon chemical cues (Mathis & Vincent 2000; Amo et al. 2004). These animals must be sensitive to gustatory and olfactory cues from predators when visual cues are either impossible or not well received. In the case of wolf spiders as threats, they actively work to diminish their visual presence while stalking prey so having the ability to pick up on their chemical cues would be beneficial (Personal Observation). This assumption has been supported when testing Wall Lizards (*Podarcis muralis*) that shelter in dark caves during the day for differences in response to chemical, visual and a combination of both cues from predatory snakes (Amo et al. 2005). *P. muralis* did not show a greater avoidance response when confronted with only visual cues or a combination of both visual and chemical cues than when exposed to only chemical cues. The effect of only receiving chemical cues (C+/V-/S-) was similar when animals were only exposed to visual cues (V+/C-/S-). The only behaviors exhibited that were higher frequencies and average durations when comparing treatment animals to conspecific control animals were antennal movement and stasis behaviors. This would signify that chemical cues alone may not be enough to elicit a behavioral response from potential predatory threat. The reason behind this could be the prey animals used in this study are only reliant upon seismic and tactile cues. As stated earlier *B. germanica* is heavily
reliant upon tactile cues due to their social nature, it could be that *A. vulgare* and *P. laevis* experience the same reliance. *A. domesticus* may need closer proximity before reacting to chemical cues. When chemical cues were added to visual cues there was no difference in reactions that could mean that neither cue is very important when reacting to predatory threat.

**Seismic Cues**

Seismic cues, like chemical cues, are likely to elicit a response regardless of the prey animal’s capability to receive visual cues. This is consistent with the expectation that these animals will need to be sensitive to vibration whether from the substrate or surrounding air. *B. germanica* was expected to react more so than the other animals as they have been documented to have a reliance upon tactile cues (Lihoreau & Rivault 2008). It would be expected for *A. vulgare* and *P. laevis* to have a similar response. *Acheta domesticus* may be likely to respond to seismic cues due to their auditory sensitivity. Crickets have two tympanal membranes on the tibia of each foreleg (Mhatre et al 2009). It is possible that within these membranes seismic cues become amplified. When allowed only seismic cues (S+/V-/C-) there were higher frequencies and average durations of walking, antennal movement, stasis and grooming behaviors in treatment animals rather than in conspecific control animals. Seismic cues alone may be enough for prey animals to react to potential predatory threat and was found to be true in all four species. This is further supported by when exposing prey animals to combinations of cues the addition of seismic cues for both visual and chemical cues lead to an increase in frequency and average durations.
V+/C+/S+

When animals were exposed to all three cues (V+/C+/S+) frequencies and average durations were significantly lower than control conspecifics when compared to every other experiment other than when only exposed to chemical cues (C+/V-/S-). This could be due to overstimulation to sensory input. Overstimulation may make it more difficult for an animal to react to several cues than when reacting to one or two. The prey animals may also react differently to all three cues being received simultaneously than they would isolated or paired. Spiny lobsters (Panulirus argus) when overstimulation of chemoreceptors has been induced mechanical and chemical transduction is shut down in the lobsters (Love-Chezem et al 2013). If overstimulation is induced from several pathways the animals could exhibit similar shutting down of different physiological responses.

No Barrier

Without a barrier it is expected that animals would not have the potential issues developed by having a barrier between predator and prey, visual skewing or not enough chemical flow through the barrier, would be eliminated. If any issues had existed they would be discovered during these experiments. Similar results would also be expected when all cues are available but with a barrier (V+/C+/S+).

Without a barrier and all three cues treatment animals exhibited higher frequencies and average durations of walking, antennal movement, stasis, running and hopping behaviors than control conspecifics and for the first time running behavior has been exhibited. This could indicate that direct contact with the predator stimulates a response in the prey.
animals without over stimulating their nervous systems. The threat may be so immediate the response is too quick to become slowed or confused by nervous response. When both predator and prey are no longer in unnatural conditions they are free to act and react as they would when confronted with each other in nature.

During the experiment without barriers the spiders made physical contact with all four species, some trials ending in predation for *B. germanica*. When spiders made physical contact with *A. vulgare* they exhibited conglobation for the first and only time during these experiments. This would suggest that physical contact is necessary for these animals to react in this way and could only be brought out in a no barrier experiment. The first and only time *A. domesticus* exhibited hopping behavior also happened during these trials and immediately following the attack by a spider. Immediate threat may be the motivator for hopping behavior as it was with conglobation in *A. vulgare*. Running behavior is *A. domesticus* as well as *B. germanica* increased during these trials, especially upon physical contact. In several trials *B. germanica* walked towards a spider while moving its antennae and upon antennal to limb contact with the spider *B. germanica* immediately turned around and ran in the opposite direction. These reactions were not exhibited in any other experiments and show the importance of how experimentation in a laboratory setting can create unnatural conditions that may change the behavior of the experimental subjects. Olfactory exposure to human males causes stress and related analgesia in rodents that may have affected years of behavioral research (Sorge et al 2014). Providing as natural a setting as possible may be crucial in understanding the true behavioral patterns of not only arthropods, but all animals.
Future studies should consider if not only specific cues affect prey behavior, but also if prey are reacting to specific behaviors by predators (i.e. do prey walk more when the predator is also walking). I collected predator behavior along with the prey behavior of this study as well as sound spectrographs of seismic trials and plan to pursue this question in the future. I would also consider whether different predators trigger different reactions in prey animals. Do prey animals respond differently to male versus female predators? Perhaps female predators emit different chemical cues that may change prey reaction. Does predator size matter in prey response? There may be a predator size range where prey react differently depending on how much larger or smaller the predator is than the prey. Prey reaction response time would also be interesting to know and how that varies with what cue they are receiving from predators. The possibility that certain cues elicit a faster or slower response time is likely, especially given the prey animal’s physiological adaptations for receiving specific cues (i.e. crickets may respond not only more frequently but faster to seismic cues). These questions are important in understanding how prey animals have evolved to detect, avoid and defend themselves against predation.

The physiological and behavioral adaptations of arthropods become clearer with a greater foundation of data and knowledge of how cues from predators drive prey behavior. Nearly all animals are potential prey and though this study focuses on arthropods, it can similarly be applied to other organisms. There may be significant differences between arthropods versus reptiles versus mammals, etc due to their different evolutionary paths,
environments and physiologies. There is a lot of room for future studies that can add to the total picture of how cues drive prey actions.

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minutes, and the black goby, Gobius niger: the effect of age and longevity. Behavioral

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Table 1. Cues tested and controlled for in each of eight experiments.

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Cues Tested</th>
<th>Cues Controlled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment 1</td>
<td>Visual</td>
<td>Chemical, Seismic</td>
</tr>
<tr>
<td>Experiment 2</td>
<td>Chemical</td>
<td>Seismic, Visual</td>
</tr>
<tr>
<td>Experiment 3</td>
<td>Seismic</td>
<td>Chemical, Visual</td>
</tr>
<tr>
<td>Experiment 4</td>
<td>Visual, Chemical</td>
<td>Seismic</td>
</tr>
<tr>
<td>Experiment 5</td>
<td>Visual, Seismic</td>
<td>Chemical</td>
</tr>
<tr>
<td>Experiment 6</td>
<td>Chemical, Seismic</td>
<td>Visual</td>
</tr>
<tr>
<td>Experiment 7</td>
<td>Visual, Chemical, Seismic</td>
<td>None</td>
</tr>
<tr>
<td>Experiment 8</td>
<td>Visual, Chemical, Seismic (no barriers)</td>
<td>None</td>
</tr>
</tbody>
</table>
Table 2. Prey actions recorded.

<table>
<thead>
<tr>
<th>Prey</th>
<th>Actions</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. domesticus</em></td>
<td>Running, Walking, Antennal movement</td>
</tr>
<tr>
<td><em>B. germanica</em></td>
<td>Running, Walking, Antennal movement</td>
</tr>
<tr>
<td><em>A. vulgare</em></td>
<td>Running, Walking, Antennal movement</td>
</tr>
<tr>
<td><em>P. laevis</em></td>
<td>Running, Walking, Antennal movement</td>
</tr>
</tbody>
</table>
Table 3. Cue totals for each species within each experiment.

<table>
<thead>
<tr>
<th></th>
<th>V+/C-/S-</th>
<th>C+/V-/S-</th>
<th>S+/V-/C-</th>
<th>V+/C+/S-</th>
<th>V+/S+/C-</th>
<th>C+/S+/V-</th>
<th>V+/C+/S+</th>
<th>Barrier</th>
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<td>2</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>3</td>
</tr>
<tr>
<td>P. laevis</td>
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<td>0</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>A. domesticus</td>
<td>3</td>
<td>3</td>
<td>4</td>
<td>3</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>B. germanica</td>
<td>1</td>
<td>0</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
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<tr>
<td>Total</td>
<td>11</td>
<td>4</td>
<td>13</td>
<td>10</td>
<td>13</td>
<td>9</td>
<td>7</td>
<td>16</td>
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</table>
Table 4. Frequencies of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual cues, but not chemical or seismic cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>V+/C-/S-behavior</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. vulgare</em></td>
<td>NS</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td><em>P. laevis</em></td>
<td>T&gt;C</td>
<td>NS</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td><em>A. domesticus</em></td>
<td>NS</td>
<td>C&gt;T</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td><em>B. germanica</em></td>
<td>NS</td>
<td>C&gt;T</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>
Table 5. Average durations of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual cues, but not chemical or seismic cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>V+/C-/S-</th>
<th>Species</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A. vulgare</td>
<td>NS</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>P. laevis</td>
<td>C&gt;T</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>A. domesticus</td>
<td>C&gt;T</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>B. germanica</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>
Table 6. Frequencies of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to chemical cues, but not visual or seismic cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>C+/V-/S- Species</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. vulgare</td>
<td>NS</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P. laevis</td>
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<td>NS</td>
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<td>NS</td>
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<td>NS</td>
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<tr>
<td>A. domesticus</td>
<td>NS</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>T&gt;C</td>
</tr>
<tr>
<td>B. germanica</td>
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</table>
Table 7. Average durations of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to chemical cues, but not visual or seismic cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>C+/V-/S- Species</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. vulgare</em></td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td><em>P. laevis</em></td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td><em>A. domesticus</em></td>
<td>NS</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td><em>B. germanica</em></td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
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</table>
Table 8. Frequencies of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to seismic cues, but not visual or chemical cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>Species</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. vulgare</em></td>
<td>NS</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td><em>P. laevis</em></td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td><em>A. domesticus</em></td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
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<tr>
<td><em>B. germanica</em></td>
<td>C&gt;T</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
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Table 9. Average durations of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to seismic cues, but not visual or chemical cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>S+/V-/C- Species</th>
<th>Behavior Average Durations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Walk</td>
</tr>
<tr>
<td>A. vulgare</td>
<td>C&gt;T</td>
</tr>
<tr>
<td>P. laevis</td>
<td>C&gt;T</td>
</tr>
<tr>
<td>A. domesticus</td>
<td>C&gt;T</td>
</tr>
<tr>
<td>B. germanica</td>
<td>C&gt;T</td>
</tr>
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</table>
Table 10. Frequencies of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual and chemical cues, but not seismic cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>V+/C+/S-</th>
<th>Behavior Frequencies</th>
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</thead>
<tbody>
<tr>
<td>Species</td>
<td>Walk</td>
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<tr>
<td>A. vulgare</td>
<td>NS</td>
</tr>
<tr>
<td>P. laevis</td>
<td>NS</td>
</tr>
<tr>
<td>A. domesticus</td>
<td>NS</td>
</tr>
<tr>
<td>B. germanica</td>
<td>NS</td>
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</table>
Table 11. Average durations of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual and chemical cues, but not seismic cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>V+/C+/S- Species</th>
<th>Behavior</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. vulgare</td>
<td></td>
<td>C&gt;T</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
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<td>A. domesticus</td>
<td></td>
<td>C&gt;T</td>
<td>T&gt;C</td>
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<td>NS</td>
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<td>B. germanica</td>
<td></td>
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<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
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Table 12. Frequencies of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual and seismic cues, but not chemical cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>Species</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. vulgare</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
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<td>NS</td>
<td>NS</td>
<td>NS</td>
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<tr>
<td>P. laevis</td>
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<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>A. domesticus</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
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<td>NS</td>
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<tr>
<td>B. germanica</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
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Table 13. Average durations of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual and seismic cues, but not chemical cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>V+/S+/C-</th>
<th>Behavior Average Durations</th>
</tr>
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<tbody>
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<td>Walk</td>
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<tr>
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<td>C&gt;T</td>
</tr>
<tr>
<td>P. laevis</td>
<td>C&gt;T</td>
</tr>
<tr>
<td>A. domesticus</td>
<td>C&gt;T</td>
</tr>
<tr>
<td>B. germanica</td>
<td>C&gt;T</td>
</tr>
</tbody>
</table>
Table 14. Frequencies of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to chemical and seismic cues, but not visual cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>C+/S+/V- Species</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
</tr>
</thead>
<tbody>
<tr>
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<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P. laevis</td>
<td>NS</td>
<td>T&gt;C</td>
<td>C&gt;T</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>A. domesticus</td>
<td>NS</td>
<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
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<tr>
<td>B. germanica</td>
<td>C&gt;T</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
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</tbody>
</table>
Table 15. Average durations of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to chemical and seismic cues, but not visual cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>C+/S+/V-</th>
<th>Behavior Average Durations</th>
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</thead>
<tbody>
<tr>
<td>Species</td>
<td>Walk</td>
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<tr>
<td>A. vulgare</td>
<td>C&gt;T</td>
</tr>
<tr>
<td>P. laevis</td>
<td>C&gt;T</td>
</tr>
<tr>
<td>A. domesticus</td>
<td>C&gt;T</td>
</tr>
<tr>
<td>B. germanica</td>
<td>C&gt;T</td>
</tr>
</tbody>
</table>
Table 16. Frequencies of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual, chemical and seismic cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>Species</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. vulgare</td>
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<td>NS</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>P. laevis</td>
<td>NS</td>
<td>NS</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>A. domesticus</td>
<td>NS</td>
<td>NS</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>B. germanica</td>
<td>C&gt;T</td>
<td>NS</td>
<td>T&gt;C</td>
<td>NS</td>
<td>NS</td>
<td>C&gt;T</td>
</tr>
</tbody>
</table>
Table 17. Average durations of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual, chemical and seismic cues from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>V+/C+/S+ Species</th>
<th>Walk</th>
<th>Ant. Mov.</th>
<th>Stasis</th>
<th>Run</th>
<th>Climb</th>
<th>Groom</th>
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</thead>
<tbody>
<tr>
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<td>NS</td>
<td>NS</td>
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<tr>
<td>P. laevis</td>
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<td>A. domesticus</td>
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<td>B. germanica</td>
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<td>T&gt;C</td>
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<td>T&gt;C</td>
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Table 18. Frequencies of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual, chemical and seismic cues without a barrier from a predatory spider. NS indicates no significant differences.

<table>
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<tr>
<th>No Barrier Species</th>
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<th>Run</th>
<th>Climb</th>
<th>Groom</th>
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<tbody>
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<td>T&gt;C</td>
<td>T&gt;C</td>
<td>NS</td>
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<td>P. laevis</td>
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<td>T&gt;C</td>
<td>T&gt;C</td>
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<td>B. germanica</td>
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<td>NS</td>
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</table>
Table 19. Average durations of treatment (T) and control (C) comparisons for each behavior where the treatment animals were exposed to visual, chemical and seismic cues without a barrier from a predatory spider. NS indicates no significant differences.

<table>
<thead>
<tr>
<th>No Barrier Species</th>
<th>Behavior Average Durations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Walk</td>
</tr>
<tr>
<td>A. vulgare</td>
<td>C&gt;T</td>
</tr>
<tr>
<td>P. laevis</td>
<td>C&gt;T</td>
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<td>A. domesticus</td>
<td>NS</td>
</tr>
<tr>
<td>B. germanica</td>
<td>C&gt;T</td>
</tr>
</tbody>
</table>
Figure 1. Photographic example (Experiment 7) of apparatus. The prey animal was placed within the clear cylinder, while the predator was placed underneath the aluminum lid at the beginning of each trial. To the left is the wire connecting the electric piezo transducer to the laptop.
Figure 2. Mean frequency of (a) walking behavior, (b) antennal movement, (c) stasis behavior and (d) grooming behavior in (A) *Armadillidium vulgare*, (B) *Porcellio laevis*, (C) *Acheta domestica* and (D) *Blatella germanica* when exposed to visual cues, but not seismic or chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 3. Mean average durations of (a) walking behavior and (b) antennal movement in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to visual cues, but not seismic or chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 4. Mean frequency of walking behavior in *Porcellio laevis* when exposed to visual cues, but not seismic or chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 5. Mean average durations of walking behavior in *Porcellio laevis* and *Acheta domesticus* when exposed to visual cues, but not seismic or chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 6. Mean frequency of antennal movement in *Armadillidium vulgare*, *Acheta domesticus* and *Blatella germanica* when exposed to visual cues, but not seismic or chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 7. Mean average durations of antennal movement in *Armadillidium vulgare*, and *Porcellio laevis* when exposed to visual cues, but not seismic or chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 8. Mean frequencies of stasis behavior in *Armadillidium vulgare*, *Porcellio laevis*, and *Acheta domesticus* when exposed to visual cues, but not seismic or chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 9. Mean frequency of (a) antennal movement, (b) stasis behavior and (c) grooming behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to chemical cues, but not seismic or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 10. Mean average durations of (a) walking, (b) antennal movement, and (c) grooming behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to chemical cues, but not seismic or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 11. Mean frequencies of antennal movement in *Armadillidium vulgare* and *Acheta domesticus* when exposed to chemical cues, but not seismic or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 12. Mean average durations of antennal movement in *Acheta domesticus* when exposed to chemical cues, but not seismic or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 13. Mean frequencies of stasis behavior in *Acheta domesticus* when exposed to chemical cues, but not seismic or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 14. Mean average durations of grooming behavior in *Acheta domesticus* when exposed to chemical cues, but not seismic or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 15. Mean frequencies of (a) walking, (b) antennal movement, (c) stasis behavior and (d) climbing behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to seismic cues, but not chemical or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 16. Mean average durations of (a) walking, (b) antennal movement, and (c) grooming behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to seismic cues, but not chemical or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 17. Mean frequencies of walking behavior in *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to seismic cues, but not chemical or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 18. Mean average durations of walking behavior in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to seismic cues, but not chemical or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 19. Mean frequencies of antennal movement in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to seismic cues, but not chemical or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 20. Mean frequencies of antennal movement in *Armadillidium vulgare*, *Porcellio laevis*, and *Blatella germanica* when exposed to seismic cues, but not chemical or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 21. Mean frequencies of stasis behavior in *Armadillidium vulgare* and *Blatella germanica* when exposed to seismic cues, but not chemical or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 22. Mean average durations of grooming behavior in *Armadillidium vulgare* and *Blatella germanica* when exposed to seismic cues, but not chemical or visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 23. Mean frequencies of stasis behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to visual and chemical cues, but not seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 24. Mean average durations of walking behavior in *Armadillidium vulgare*, *Porcellio laevis*, and *Acheta domesticus* when exposed to visual and chemical cues, but not seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 25. Mean frequencies of antennal movement in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual and chemical cues, but not seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 26. Mean average durations of antennal movement in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual and chemical cues, but not seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 27. Mean frequencies of stasis behavior in *Porcellio laevis* and *Acheta domesticus* when exposed to visual and chemical cues, but not seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 28. Mean frequencies of (a) walking, (b) antennal movement, (c) stasis behavior, (d) climbing behavior and (e) grooming behavior in (A) *Armadillidium vulgare*, (B) *Porcellio laevis*, (C) *Acheta domesticus* and (D) *Blatella germanica* when exposed to visual and seismic cues, but not chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 29. Mean frequencies of walking in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual and seismic cues, but not chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 30. Mean average durations of walking in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual and seismic cues, but not chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 31. Mean frequencies of antennal movement in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual and seismic cues, but not chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 32. Mean average durations of antennal movement in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual and seismic cues, but not chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 33. Mean average durations of (a) walking, (b) stasis behavior, (c) climbing behavior, and (d) grooming behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to visual and seismic cues, but not chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 34. Mean frequencies of stasis behavior in *Acheta domesticus* when exposed to visual and seismic cues, but not chemical cues from a predatory spider. Error bars represent standard error on the means.
Figure 35. Mean frequencies of (a) walking, (b) antennal movement and, (c) stasis behavior in (A) *Armadillidium vulgare*, (B) *Porcellio laevis*, (C) *Acheta domesticus* and (D) *Blatella germanica* when exposed to chemical and seismic cues, but not visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 36. Mean average durations of (a) antennal movement and (b) stasis behavior in (A) *Armadillidium vulgare*, (B) *Porcellio laevis*, (C) *Acheta domesticus* and (D) *Blatella germanica* when exposed to chemical and seismic cues, but not visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 37. Mean frequencies of walking in *Blatella germanica* when exposed to chemical and seismic cues, but not visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 38. Mean average durations of walking in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to chemical and seismic cues, but not visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 39. Mean frequencies of antennal movement in Armadillidium vulgare, Porcellio laevis, Acheta domesticus and Blatella germanica when exposed to chemical and seismic cues, but not visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 40. Mean average durations of antennal movement in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to chemical and seismic cues, but not visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 41. Mean frequencies of stasis behavior in *Porcellio laevis* and *Acheta domesticus* when exposed to chemical and seismic cues, but not visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 42. Mean average durations of stasis behavior in *Porcellio laevis* and *Acheta domesticus* when exposed to chemical and seismic cues, but not visual cues from a predatory spider. Error bars represent standard error on the means.
Figure 43. Mean frequencies of (a) walking, (b) antennal movement, (c) stasis behavior, and (d) grooming behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 44. Mean average durations of (a) walking, (b) antennal movement, and (c) grooming behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 45. Mean frequencies of walking in *Blatella germanica* when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 46. Mean average durations of walking in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 47. Mean frequencies of stasis behavior in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 48. Mean average durations of stasis behavior in *Porcellio laevis* and *Acheta domesticus* when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 49. Mean frequencies of climbing behavior in *Blatella germanica* when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 50. Mean average durations of climbing behavior in *Blatella germanica* when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 51. Mean frequencies of grooming behavior in *Blatella germanica* when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 52. Mean average durations of grooming behavior in *Blatella germanica* when exposed to visual, chemical and seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 53. Mean frequencies of (a) antennal movement, (b) running, and (c) stasis behavior in, and (d) grooming behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domestica and (D) Blatella germanica when exposed to visual, chemical and seismic cues without a barrier from a predatory spider. Error bars represent standard error on the means.
Figure 54. Mean frequencies of walking in *Armadillidium vulgare*, *Porcellio laevis*, and *Acheta domesticus* when exposed to visual, chemical and seismic cues without a barrier from a predatory spider. Error bars represent standard error on the means.
Figure 55. Mean average durations of walking in *Armadillidium vulgare*, *Porcellio laevis*, and *Blatella germanica* when exposed to visual, chemical and seismic cues without a barrier from a predatory spider. Error bars represent standard error on the means.
Figure 56. Mean frequencies of antennal movement in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual, chemical and seismic cues without a barrier from a predatory spider. Error bars represent standard error on the means.
Figure 57. Mean average durations of antennal movement in *Armadillidium vulgare*, *Porcellio laevis*, *Acheta domesticus* and *Blatella germanica* when exposed to visual, chemical and seismic cues without a barrier from a predatory spider. Error bars represent standard error on the means.
Figure 58. Mean average durations running behavior in *Acheta domesticus* when exposed to visual, chemical and seismic cues without a barrier from a predatory spider. Error bars represent standard error on the means.
Figure 59. Mean average durations running behavior in *Acheta domesticus* when exposed to visual, chemical and seismic cues without a barrier from a predatory spider. Error bars represent standard error on the means.
Figure 60. Mean frequencies of stasis behavior in *Porcellio laevis* and *Acheta domesticus* when exposed to visual, chemical and seismic cues without a barrier from a predatory spider. Error bars represent standard error on the means.
Figure 61. Mean frequencies of hopping behavior in *Acheta domesticus* when exposed to visual, chemical and seismic cues without a barrier from a predatory spider. Error bars represent standard error on the means.
Figure 62. Mean frequencies of (a) walking, (b) antennal movement, (c) stasis behavior in, (d) climbing behavior, and (e) grooming behavior in (A) *Armadillidium vulgare*, (B) *Porcellio laevis*, (C) *Acheta domesticus* and (D) *Blatella germanica* when exposed to no visual, chemical or seismic cues from a predatory spider. Error bars represent standard error on the means.
Figure 63. Mean average durations of (a) antennal movement, (b) climbing behavior, and (c) grooming behavior in (A) Armadillidium vulgare, (B) Porcellio laevis, (C) Acheta domesticus and (D) Blatella germanica when exposed to no visual, chemical or seismic cues from a predatory spider. Error bars represent standard error on the means.